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Trehalose induced by reactive oxygen species relieved the radial growth defects of *Pleurotus ostreatus* under heat stress

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Abstract
Trehalose is a nonreducing disaccharide, and it plays an intracellular protective role in organisms under various stress conditions. In this study, the trehalose synthesis and its protective role in *Pleurotus ostreatus* were investigated. As a signal in metabolic regulation, reactive oxygen species (ROS) accumulated in the mycelia of *P. ostreatus* under heat stress (HS). Furthermore, mycelial growth was significantly inhibited, and the malondialdehyde (MDA) level significantly increased under HS. First, exogenous addition of H_2O_2 inhibited mycelial growth and elevated the MDA level, while *N*-acetyl cysteine (NAC) and vitamin C (VC) reduced the MDA level and recovered mycelial growth under HS by scavenging ROS. These results indicated that the mycelial radial growth defect under HS might be partly caused by ROS accumulation. Second, adding NAC and VC to the media resulted in rescued trehalose accumulation, which indicated that ROS has an effect on inducing trehalose synthesis. Third, the mycelial growth was recovered by addition of trehalose to the media after HS, and the MDA level was reduced. This effect was further verified by the overexpression of genes for trehalose-6-phosphate synthase (*TPS*) and neutral trehalase (*NTH*), which led to increased and reduced trehalose content, respectively. In addition, adding validamycin A (NTH inhibitor) to the media promoted trehalose accumulation and the recovered mycelial growth after HS. In conclusion, trehalose production was partly induced by ROS accumulation in the mycelia under HS, and the accumulated trehalose could promote the recovery of growth after HS, partly by reducing the MDA level in the mycelia.

Keywords Trehalose · Heat stress · Growth inhibition rate · MDA · ROS

Introduction

Oyster mushrooms (*Pleurotus ostreatus*) are one of the most widely cultivated types of mushrooms in China and East Asia (Sanchez 2010). Their commercial value is well known, not only because of their good taste and rich nutritional value but also because of their antiproliferative, antihepatoma, and antisarcoma activities (Wang et al. 2000; Lavi et al. 2006). High temperature is one of the major environmental factors that influences nearly all biological processes in microorganisms. The optimal temperature for the mycelial growth of *P. ostreatus* is between 25 °C and 30 °C, while a downshift of 5–10 °C is often required for fruiting (Kashangura 2008; Boddy et al. 2014). In China, *P. ostreatus* is usually cultivated in sheds, which results in difficulty controlling temperature, humidity, and other environmental conditions. Since not all mushroom growers have optimal climate control, elevated temperatures during summer periods can be problematic. Heat stress (HS) for several days can inhibit the mycelial growth, impair fruiting, and negatively affect mushroom quality (Chang and Miles 2004). Therefore, it is of substantial importance to investigate the mechanisms of HS response and heat resistance of *P. ostreatus*.

HS response and its mechanisms have been reported in many organisms. Throughout plant ontogenesis, the production of reactive oxygen species (ROS) is one of the main responses under HS (Wahid et al. 2007). In microbial cells, massive ROS accumulation occurs under abiotic stresses,

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